Life History Characteristics of Smallmouth Bass Populations in Nova Scotia Based on Tournament Monitoring

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Abstract

A four-year monitoring program of bass tournaments was used to describe smallmouth bass (*Micropterus dolomieu*) growth and mortality in Nova Scotia. Length and scale samples collected during tournament weigh-in at thirteen lakes and impoundments were used to summarize age, growth and mortality. Scale samples were also collected from a lake not used as a tournament site. The conceptual requirement of a trade-off between growth and reproduction was the basis on which life history patterns of smallmouth bass were addressed. The von Ber: .anffy growth model was used to represent this trade-off and parameters, such as asymptotic size and the growth coefficient, were used within the framework of life history invariants for inferring size at maturity. Estimates for size at maturity fell within known ranges for smallmouth bass after uncovering the life history invariant of relative size at maturity (L_{mat}/L_{∞}=0.6) for this data set. Production-to-biomass ratios (P/B) were determined for each population based on inferred weight at maturity. The mean P/B ratio for Nova Scotia smallmouth bass matched a P/B ratio for this species from other life history data. Instantaneous natural mortality rate, estimated by doubling the von Bertalanffy growth coefficient (M=2*K), closely matched estimates provided by a review of North American data on age and growth of smallmouth bass. Fish community structure appears to play a role in determining asymptotic size of smallmouth bass in Nova Scotia. The presence of chain pickerel (*Esox niger*), as well as sites with only one other co-existing fish species, generally result in lower asymptotic size for smallmouth bass.

Introduction

An effective monitoring program for determining intra-specific life history variation in fish would employ a sampling gear in a consistent fashion across a wide area of the species range as well as achieving broad spatial coverage within any single population. Bass tournaments meet these criteria because competitors 'sample' over a large area of a single water body and tournaments are a relatively common occurrence in many different locations in North America. Sampling tournament-caught bass for calcified tissue provides basic data on age, size and survival upon which other life history parameters can be reasonably inferred. This inference stems largely from an energetic trade-off between growth and reproduction that leads to invariant scaling among other parameters such as maturity, growth rate and mortality (Charnov 1993).

The von Bertalanffy growth model represents this trade-off reasonably well. The growth rate, as represented by the Brody growth coefficient (K), is inversely proportional to asymptotic size such that a high rate of growth leads to smaller asymptotic size. This inverse relationship reflects the allocation of energy to maturation that defines the boundary between juvenile and adult life stages. Three life history patterns relevant to this study occur among fish populations within taxonomic groupings based on a trade-off between growth and reproduction (Beverton 1992). First, the instantaneous mortality rate is positively correlated with the growth coefficient such that the ratio of these two parameters is relatively constant. Second, length at maturity is positively correlated with the von Bertalanffy asymptotic length. Third, the von Bertalanffy growth coefficient and asymptotic length are negatively correlated. Together these three patterns are collectively referred to as Beverton-Holt invariants (Charnov 1993).

The trade-off between growth and reproduction is also important for determining production-to-biomass ratios (P/B). Fish size-at-maturity and longevity are inversely proportional to P/B ratios and can be predicted from weight at maturity (Randall and Minns 2000). Since growth conditions vary among populations, the trade-off between growth and reproduction results in population-specific weights at maturity that in turn determines population-specific P/B ratios (Randall et al 1995; Randall and Minns 2000).

The objective of this study is to highlight the use of tournaments as a means of acquiring basic life history information necessary for characterizing bass populations. This kind of information has long been advocated as an important contribution from bass tournaments (e.g., Schramm et al. 1991). Our purpose is twofold. First, we show that more general levels of insight are possible when one applies patterns in life history invariants and P/B ratios to data readily accessible from routine monitoring of tournaments. Second, the life history comparison is based on tournament monitoring in Nova Scotia, an area with little or no published information on smallmouth bass ecology.

The life history characteristics of smallmouth bass in Nova Scotia are compared to the larger latitudinal survey of smallmouth bass life history assembled by Beamesderfer and North (1995). In particular, we compare our estimates of von Bertalanffy growth parameters and natural mortality with those detected in that broader survey.

Methods

Smallmouth bass tournaments were monitored in 1995-98 in a number of locations in Nova Scotia (Table 1). Tournaments were held during the months of May through October with minimum length limits ranging from "no limit" to 254 mm. Catch limits were set according to individual angler or two-angler teams and ranged from one to six smallmouth bass per team. Scale samples were removed from a subset of bass (stratified in 2 cm length intervals) for aging purposes and the lengths of all bass weighed-in at the tournament were recorded.

Weigh-in stations for live fish were used at each lake. At each station, individual smallmouth bass were received after official weigh-in and total length (mm) and weight (nearest gram) were recorded. For most tournaments, all fish were weighed but in some cases random samples of fish were drawn from the holding tank in situations where weight of all fish could not be completed in a reasonable time period. Scales were collected from a subset of smallmouth bass in each tournament that covered the size range of fish captured.

Scales or scale impressions were read by an experienced technician with a sample of scales and ages provided to two independent experts for comparison. Estimated ages differing by more than one year were rejected. From this data, mean length at age for each population were developed that served to partition length frequency data into age groups.

Mean length-at-age data and age frequency distributions were used to calculate a number of life history parameters. Total annual survival was estimated by the catch curve method of Robson and Chapman (1961). Asymptotic length and the growth

coefficient in the von Bertalanffy growth equation were estimated using the mean length-at-age data. The form of the von Bertalanffy equation was:

$$L_t = L_\infty(1-\exp(-K(t-t_0)))$$

Estimates of t_0 and length at ages not included in the tournament data (age 1 and 2) were based on data from Beamesderfer and North (1995). The estimate of t_0 (=-0.004) represented the mean value based on the smallmouth bass life history compilation of Beamesderfer and North (1995). The mean length at age for each of the populations is listed in Appendix 1.

One of the key assumptions for Beverton-Holt invariants is that the von Bertalanffy growth model represents a trade-off between early growth and asymptotic size (Charnov 1993). Fast early growth leads to small asymptotic size while slow early growth leads to larger asymptotic size. A plot of $\log_e K$ vs. $\log_e L_\infty$ for taxonomic groupings of fish has a negative slope, h (=absolute value of slope), representing this trade-off (Charnov 1993). Since the net reproductive rate (lifetime production of offspring) is a function of both age of maturity and the growth coefficient, Charnov (eq. 4.2; 1993) demonstrated that h has an important role in Beverton-Holt invariants;

$$h = (R-1/R)*\log_e(1-R)$$

where R is a ratio of size at maturity relative to asymptotic size ($R = L_{mat} / L_\infty$). We used geometric mean regression to estimate the slope (h = absolute value of slope) of the negative relationship between the growth coefficient, K, and asymptotic size, L_∞, that in turn was used to determine the relative size of maturity, R. The relative size at maturity can also be estimated based on the growth coefficient and age of maturity (Charnov & Berrigan 1991; Beverton 1992; Charnov 1993):

$$R = 1 - e^{-K*\alpha}$$

where α is the age of maturity. In Ontario, egg development in females reaches mature stages at age 5 and certainly by age 6 (Scott and Crossman 1973; Post 1982; Orendorff 1983). In this analysis, α=5 was used as the age of maturation for each population and was combined with population-specific growth coefficients (K) for estimating R for each population. With the relative size at maturity (R), L_{mat} was then inferred based on the estimated L_{∞} for each population. The inferred length at maturity for each population was converted to weight at maturity (W_{mat}) by the regression (Randall and Minns 2000):

$$\log_{10}(W_{mat}) = -4.61 + 2.92(\log_{10}(L_{mat}))$$

where L_{mat} is FL (mm) and weight is wet weight (g). Total lengths were converted to fork lengths based on relationships in Carlander (1977; TL = 1.04*FL). Finally, W_{mat} for each Nova Scotia population was used to calculate production-to-biomass ratios based on the relationship (Randall and Minns 2000):

$$P/B = 2.64(W_{mat}^{-0.35}).$$

The ratio of adult instantaneous mortality rate to the growth coefficient (Z/K based on Ricker's (1975) parameter symbols and M/K based on Charnov's (1993) parameter symbols) is a Beverton-Holt invariant. This ratio is in the range of 1.65 - 2.01 (Pauly 1980; Charnov 1993). Based on the estimates for *h* and R in this study (Beverton 1992; Fig. 4.15 in Charnov 1993), an estimate of M/K was used for purposes of comparison among Nova Scotia smallmouth bass populations.

No empirical estimates of instantaneous natural morality (M; Ricker 1975) are available for smallmouth bass in Nova Scotia. The median value for M is 0.39 in North America (Beamesderfer and North 1995). This value is close to the empirical estimate of

0.30 (± 0.11, 95% CI; Shuter et al 1985) from the long-term study of smallmouth bass population ecology in Lake Opeongo. In this study, we used M=0.39 for our estimate of instantaneous natural mortality for smallmouth bass in Nova Scotia and later compare this to inferred values of M from the Beverton-Holt life history invariant (M/K=2).

Relative weight (Anderson and Newman 1996) and catch-per-unit-effort data were assessed for each tournament for fish greater that 253 mm (TL; MacMillan and Robinson 1999). Relative weight was calculated using the standard weight equation for smallmouth bass:

$$\text{Log}_{10}W_s = -5.329 + 3.20\text{Log}_{10}L$$

where W_s = standard weight and L = length (mm), as described in Kolander et al (1993).

Catch and effort data were collected for all tournaments. Organizers were required to fill out a tournament summary form where they recorded the number of anglers participating, the number of fish eligible for weigh-in per day, the total number of fish weighed-in, and the numbers of hours fished. Organizers also recorded the minimum size for weigh-in (if any). Angler effort was estimated in terms of total tournament angler hours per hectare of lake. Tournament summary information was used to calculate catch-per-unit-effort (CPUE) for each tournament. The total number of smallmouth bass (>253 mm TL) was divided by the total number of hours angled to calculate the tournament estimate for the number of smallmouth bass caught per hour of angling.

Incomplete length and weight data sets were collected from several tournaments to reduce handling stress on fish. The proportion of smallmouth bass larger than 253 mm TL from incomplete data sets was used to extrapolate the number of smallmouth bass

larger than 253 mm from total catches reported in tournament summary information. This value was then used in the calculation of the number of smallmouth bass (>253 mm TL) caught per angler hour. In seven lakes, CPUE was calculated for each year of the four year study and analysis of variance was used to assess changes in CPUE over this time period.

Results

Age and Growth: Figure 1 illustrates the distribution (median, quartiles and maximum/minimum) of mean total length at ages of smallmouth bass captured in tournaments in all thirteen lakes. Sizes at young ages, particularly 3 year-olds, are somewhat higher than lengths recorded from netting and electrofishing gear for these populations (McNeill 1995). The relative weight for smallmouth bass ranged from 73 to 86 (mean, 77.3; Table 2) with most values below the 25th percentile observed for North America (W_r = 86; Beamesderfer and North 1995).

Estimates of von Bertalanffy growth parameters (K and L_∞) also reflect the relatively unproductive aspect of Nova Scotia smallmouth bass populations (Table 2). One lake in particular, George Lake, had very low growth rates for smallmouth bass and size at age data did not fit a von Bertalanffy growth model when all size data was incorporated (see Appendix 1). The oldest ages were excluded from the final growth model for George Lake and only size at age data up to age 8 are included in the final estimates (Table 2). The growth coefficient, K, ranged from 0.123 to 0.352 (mean, 0.191; 95% CI, 0.151- 0.231) covering most of the range of this parameter observed by Beamesderfer and North (1995). The median value for the growth coefficient in Nova

Scotia (K=0.18) was close to the median value for North America (K=0.16, Beamesderfer and North 1995). The estimates of L_∞ for Nova Scotia populations (range, 45.2-55.6 cm) fell largely to the lower end of the North American distribution (median, 58.5 cm; quartiles, 50.2-66.9 cm; Beamesderfer and North 1995). When taken together, the data on relative growth and the von Bertalanffy parameters, K and L_∞, clearly indicate that Nova Scotia smallmouth bass are average to below average in their growth when compared to North American data (Beamesderfer and North 1995).

Given the trade-off between growth and maximum size, it is possible to use life history invariants to provide defensible estimates of size at maturity, L_{mat}, based on von Bertalanffy parameters (Charnov and Berrigan 1991; Beverton 1992; Charnov 1993). The Nova Scotia data set demonstrates the negative relationship between the growth coefficient and maximum size under the trade-off assumption (Figure 2). The slope of the geometric mean regression in this relationship (-0.62; se, 0.08) can be used to determine the ratio, L_{mat}/L_∞, because of the inverse relationship between h (absolute value of slope) and R, the relative size at maturity (equation 4.2 and Figure 4.15 in Charnov 1993). The ratio of L_{mat}/L_∞ for Nova Scotia smallmouth bass is 0.59. This is close to an empirical estimate L_{mat}/L_∞ observed for eastern Canadian fish in general (mean, 0.53; 95% CI, 0.5-0.6; Randall and Minns 2000). Based on an age of maturity of 5 years, and population-specific values of K (Table 2), the mean value of R is 0.60 for all thirteen populations (95%CI, 0.53-0.67). Considering our estimates of h and R, as well as the upper confidence interval of the estimate for eastern Canadian fish, a value of $L_{mat}/L_\infty = 0.6$ was selected for inferring length at maturity of smallmouth bass in this data

set. Estimates of L_{mat} ranged from 245 mm to 335 mm (mean, 294 mm TL; 95% CI, 275-312, Table 2).

Population-specific estimates of W_{mat} were calculated from the general length/weight regression for smallmouth bass (Randall and Minns 2000). These estimates were used to calculate population-specific estimates of the P/B ratio (Table 2). P/B ratios varied from 0.28 to 0.39 (mean, 0.33; 95% CI, 0.31 - 0.35, Table 2).

Survival: Robson-Chapman estimates of annual survival (S) covered a broad range of values (median, 0.509; quartiles, 0.450-0.548; Table 3). Converting to instantaneous total mortality (Z) demonstrated that some populations are experiencing high levels of mortality (mean, 0.705; 95% CI, 0.606-0.805; Table 3). Using the median North American value for instantaneous natural mortality (M=0.39), we determined the instantaneous fishing mortality (F) by difference (Z=M+F; Table 3). Again, George Lake was the exception to this pattern because of its low growth rate and small asymptotic length. For George Lake, the upper quartile of instantaneous natural mortality (M=0.59) in North America was used to determine F (Beamesderfer and North 1995). Under these assumptions, instantaneous fishing mortality represented on average 40.4% of instantaneous total mortality (mean F, 0.300; 95% CI, .212-.388; Table 3). The mean exploitation rate (F*A/Z) for Nova Scotia populations is 20.95% (95% CI, 15.61-26.28; Table 3).

The assumption that the median value of M for North America is an appropriate estimate of instantaneous natural mortality for Nova Scotia populations of smallmouth bass can be examined using a life history invariant. The ratio of adult instantaneous mortality to the von Bertalanffy growth coefficient (M/K, using Charnov's (1993)

parameter symbols) has a value of 2 (e.g., Charnov 1993; Shuter et al 1998). With h = 0.62 and R = 0.60, a reasonable estimate of M/K = 2 can be used for Nova Scotia populations of smallmouth bass. Therefore, doubling the von Bertalanffy growth coefficient can be used as an estimate of instantaneous mortality (M = 2*K). Following this procedure, the estimate of M (mean, 0.383; 95% CI, 0.302-0.463; Table 4) is close to the median estimate of instantaneous natural mortality (0.39) for North America. Population-specific estimates of M for Nova Scotia represent, on average, 93% of the median values used in this study from North America (M = 0.39; George Lake M = 0.59). However, it also indicates that the population-specific estimate of M is approximately 56% of Z as determined by the Robson-Chapman estimator. The estimate of instantaneous mortality based on the life history invariant, M/K, most closely resembles the instantaneous natural mortality rather than instantaneous total mortality.

Utilizing the population-specific estimates of M as estimates of instantaneous natural mortality leads to new estimates of fishing mortality (mean, 0.323; 95% CI, 0.214-0.431) and exploitation rate (mean, 22.63%; 95% CI, 15.60-29.66; Table 4). The correlation between estimates of F based on North American estimates of M (Table 3) and estimates of F based on doubling the von Bertalanaffy growth coefficient ($F_{M=2*K}$) was significant (r_s = 0.77; $F_{M=2*K}$ = 0.02+1.02*F).

Catch and Effort: The mean angler effort in tournaments was 15.48 angler hours per ha (95% CI, 7.95-23.02) and the mean catch rate was 0.21 fish per tournament angler hour (95% CI, 0.17-0.26). There was no correlation between the general estimate of exploitation rate (Table 3) and either angler effort in tournaments or catch rate in tournaments. Similarly, there was no correlation between fishing mortality (F; Table 3)

and angler effort or catch rate in tournaments. Losses of smallmouth bass in these tournaments appear to be insufficient to influence population estimates of fishing mortality or exploitation rate.

Discussion

Biological data collected from routine monitoring of tournaments provided the foundation for characterizing the life history of Nova Scotia populations of smallmouth bass. Utilizing life history invariants provided the means of inferring parameter values related to size at maturation (Beverton 1992; Charnov and Berrigan 1991; Charnov 1993), that in turn provided an estimate of P/B for each population (Randall and Minns 2000). The mean P/B ratio inferred in this summary of life history data for smallmouth bass in Nova Scotia (mean = 0.33) matches a P/B estimate for this species from a separate life history analysis (P/B = 0.33; Randall and Minns 2000). A similar match was found between the estimates of instantaneous natural mortality based on a review of North American data (Beamesderfer and North 1995), which were used initially (Table 3), and the inferred estimate of M based on life history invariants (Table 4). Based on this study, doubling the Brody growth coefficient, K, provides a reasonable estimate of natural mortality for smallmouth bass.

Analysis of readily available age and growth data permits a detailed comparison of intra-specific life history patterns that stem largely from the trade-off between growth and reproduction occurring at the onset of maturity (Charnov and Berrigan 1991; Beverton 1992; Charnov 1993). In this study, this approach was used to estimate the length at maturity. The range in size at maturity in Nova Scotia matches the range observed in other studies (Carlander 1977; Mackereth 1995). An empirical estimate of length at maturity can certainly be gained by examining the developmental stages of ova in females. However, since smallmouth bass appear to be monogamous (Gross and Kapusinski 1997; Mackereth 1995), egg counts in nests of males provide the information

necessary to infer female maturation by relating the egg count to a general female size and fecundity relationship (Raffetto et al 1990).

Data sources for constructing life history comparisons among black bass are available from sampling fish captured in tournaments. Biological sampling was recommended in some of the first summaries of tournament data (Holbrook 1975) and the insights gained in this inter-population comparison clearly point to a renewed emphasis on sampling for age and growth information. However, tournament monitoring has largely been based on self-reporting of information for the purpose of determining fishing effort and catch rates (van Horn and Birchfield 1981; Chapman and Fish 1983; Willis and Hartman 1986).

One concern is that tournaments impose a level of mortality on bass populations (Weathers and Newman 1997; Wilde 1998). Smallmouth bass populations in Nova Scotia that are the focus of tournament activity do not appear to be governed by any losses that may be occurring as a result of this activity. In general, losses of black bass in tournaments are a function of temperature effects that occur during the handling of fish on the day of the tournament and to a lesser extent in the period immediately after the tournament (Wilde 1998). In the north, this temperature effect is relatively small when compared to warmer conditions in the southern parts of the black bass range (Kwak and Henry 1995). However, catch and release fishing can have detectable mortality consequences for black bass in the absence of any tournament activity (Storey and Ott 1994).

The von Bertalanffy growth model was used in this study as a representation of the trade-off between growth and reproduction. Others have emphasized the lack of a

strong conceptual basis for employing the von Bertalanffy model in this way and have argued for a mix of a power function for pre-maturation growth in weight followed by an asymptotic model for post-maturation growth in weight (Day and Taylor 1997). The empirical success of the von Bertalanffy model, which reinforces its traditional role in fisheries science, does have its limits. Incorporating all sizes of smallmouth bass in George Lake did not provide for a good fit to the von Bertalanffy model. The largest individuals had to be excluded to achieve an acceptable fit (Appendix 1). This may point to a mixed, two-stage model as being more effective in accounting for pre- and post-maturation growth.

Although the asymptotic size of smallmouth bass in Nova Scotia covers a wide range (Table 2), one consistent pattern emerges. With the exception of Killam Lake, all other smallmouth bass populations where L_∞ is less than 50 cm co-exist with chain pickerel. In Spectacle and George Lakes, chain pickerel is the only other fish species present. In Grand and Milo Lakes, other species such as striped bass (*Morone saxatilis*) co-exist with smallmouth bass in addition to chain pickerel. Other Nova Scotia lakes exhibit similar apparent influences of the fish community. In Elliott Lake (McNeill 1995), smallmouth bass have an asymptotic size similar to George Lake (Elliott Lake: 44°56'N;65°11'W; L_∞=27.8 cm, K=0.34) and co-exist with brown trout (*Salmo trutta*) only. In contrast, Gaspereau Lake has an L_∞ of 53.1 cm for its smallmouth bass population and co-exists with white perch (*Morone americana*) only. In Ontario, smallmouth bass in Provoking Lake (45°30'N; 78°29' W) co-exist with a sparse population of yellow perch (*Perca flavescens*) only and have a relatively low asymptotic size (Orendorff 1983; L_∞=38.2).

Together, this information points to food web structure as a key component in life history variation in smallmouth bass. The low asymptotic size of smallmouth bass in the presence of chain pickerel in Nova Scotia may signal competition between these two littoral zone predators that effectively reduces the size of adult smallmouth bass. In general, whether co-existing with efficient littoral zone predators like chain pickerel or in simple communities with only one other fish species, the lack of large size in smallmouth bass likely reflects their trophic position within the lake. In lake trout (*Salvelinus namaycush*), small asymptotic size generally corresponds to populations without pelagic prey with the reduced size reflecting increased levels energy committed to foraging activity for small prey items and away from growth (Pazzia et al. In prep.).

Intra-specific comparisons of fish growth and maturation have proven successful in accounting for life history variation among populations. Comparisons among populations of walleye (*Stizostedion vitreum*; Colby and Nepszy 1981), arctic charr (*Salvelinus alpinus*; Vøllestad and L'Abée-Lund 1994; Mangel 1996), lake trout (Shuter et al. 1998), and threespine stickleback (*Gasterosteus aculeatus*; Poizat et al. 1999; Huntingford et al. 2001) have all confirmed the theoretical framework of life history variation in fish. As this study demonstrates, monitoring bass tournaments can provide similar data needed to make life history comparisons among populations. This information can provide fishery managers with defensible estimates of natural and fishing mortality as well as exploitation rate and population-specific P/B ratios. Information of this kind could be used for conservation measures and actions for specific populations.

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References

Anderson, R.O., and R.M. Newman. 1996. Length, weight, and associated structural indices. Pages 447-482 *In* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Beamesderfer, R.C.P., and J.A. North. 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North American Journal of Fisheries Management 15: 688-704.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. Journal of Fish Biology 41 (Supplement B): 137-160.

Carlander, K.D. 1977. Handbook of freshwater fishery biology, vol. 2. Life history data on centrarchid fishes of the United States and Canada. Iowa State University Press, Ames, Iowa.

Chapman, P., and W.V. Fish. 1983. Largemouth bass tournament catch results in Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 37: 495-505.

Charnov, E.L. 1993. Life history invariants. Some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford, U.K.

Charnov, E.L., and D. Berrigan. 1991. Dimensionless numbers and the assembly rules for life histories. Philosophical Transactions of the Royal Society, London B 332: 41-48.

Day, T., and P.D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. American Naturalist 149: 381-393.

Gross, M.L., and A.R. Kapuscinski. 1997. Reproductive success of smallmouth bass estimated and evaluated from family-specific DNA fingerprints. Ecology 78: 1424-1430.

Holbrook, J.A. 1975. Bass fishing tournaments. Pages 408-415 *In* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Huntingford, F.A., S. Chellappa, A.C. Taylor, and R.H.C. Strang. 2001. Energy reserves and reproductive investment in male three-spined sticklebacks, *Gasterosteus aculeatus*. Ecology of Freshwater Fish 10: 111-117.

Kolander, T.D., D.W. Willis, and B.R. Murphy. 1993. Proposed revision of the standard weight (W_s) equation for smallmouth bass. North American Journal of Fisheries Management 13: 398-400.

Kwak, T.J., and M.G. Henry. 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. North American Journal of Fisheries Management 15: 621-630

McNeill, A.J. 1995. An overview of the smallmouth bass in Nova Scotia. North American Journal of Fisheries Management 15: 680-687.

Mackereth, R.W. 1995. Size-based variation in the allocation of energy to parental care by male smallmouth bass (*Micropterus dolomieu*). Ph. D. Thesis, University of Guelph.

Mangel, M. 1996. Life history invariants, age at maturity and the ferox trout. Evolutionary Ecology 10: 249-263.

Orendorff, J.A. 1983. The relationships of feeding, growth and maturation in three northern smallmouth bass, *Micropterus dolomieui*, Lacépède, populations. M.Sc. thesis, University of Toronto.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. Journal de Conseil International Exploration de la Mer 39: 175-192.

Pazzia, I., M. Trudel, M. Ridgway, and J.B. Rasmussen. (In Prep.). Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*).

Poizat, G., E. Rosecchi, and A.J. Crivelli. 1999. Empirical evidence of a trade-off between reproductive effort and expectation of future reproduction in female three-spined sticklebacks. Proceedings of the Royal Society of London, B 266: 1543-1548.

Post, E.E. 1982. Some factors influencing the reproductive effort of smallmouth bass in two Ontario lakes. M.Sc. thesis, University of Toronto.

Raffetto, N.S., J.R. Baylis, and S.L. Serns. 1990. Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieui*). Ecology 71: 1523-1535.

Randall, R.G., and C.K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57: 1657-1667.

Randall, R.G., J.R.M. Kelso, and C.K. Minns. 1995. Fish production in freshwaters: are rivers more productive than lakes? Canadian Journal of Fisheries and Aquatic Sciences 52: 631-643.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.

Ridgway, M.S., and B.J. Shuter. 1996. Effects of displacement on the seasonal movements and home range characteristics of smallmouth bass in Lake Opeongo. North American Journal of Fisheries Management 16: 371-377.

Scott,W.B., and E.J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin 184, Fisheries Research Board of Canada.

Robson, D.S., and D.G. Chapman. 1961. Catch curves and mortality rates. Transactions of the American Fisheries Society 90: 181-189.

Schramm, H.L., Jr., and nine co-authors. 1991. Sociological, economic, and biological aspects of competitive fishing. Fisheries 16: 13-21.

Shuter, B.J., J.E. Matuszek, and H.A. Regier. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieu*), 1936-83. Canadian Journal of Fisheries and Aquatic Sciences 44: 229-238.

Shuter, B.J., M.L. Jones, R.M. Korver, and N.P. Lester. 1998. A general, life history model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55: 2161-2177.

Storey, K.W., and R.A. Ott, Jr. 1994. The largemouth bass catch-and-release regulation in a new reservoir, Purtis Creek State Park Lake, Texas. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 46(1992): 377-385.

Van Horn, S.L., and L.J. Birchfield. 1981. The North Carolina largemouth bass catch survey. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 35: 433-459.

Vøllestad, L.A., and J.H. L'Abée-Lund. 1994. Evolution of the life history of arctic charr *Salvelinus alpinus*. Evolutionary Ecology 8: 315-327.

Weathers, K.C., and M.J. Newman. 1997. Effects of organizational procedures on mortality of largemouth bass during summer tournaments. North American Journal of Fisheries Management 17: 131-135.

Wilde, G.R. 1998. Tournament-associated mortality in black bass. Fisheries 23(10): 12-22.

Willis, D.W., and R.F. Hartman. 1986. The Kansas black bass tournament monitoring program. Fisheries 11: 7-10.

Table 1. Site locations and characteristics including year of smallmouth bass introduction and lake designation as either natural or impoundment.

Site	Location Lat/Long	Surface Area (ha)	Maximum Depth (m)	Introduction Date	Type
Grand	44°70'N/ 64°24'W	1,940	41	1961[b]	Natural
Porters	44°45'N/ 63°18'W	1,651	23	1988[b]	Natural
Panuke	45°50'N/ 64°05'W	1,639	35	1983[b]	Impoundment
Gaspereau	44°57'N/ 64°32'W	860	NA[a]	1968	Impoundment
Black R	44°56'N/ 64°24'W	668	12	1967	Impoundment
OPP	44°03'N/ 65°54'W	586	18	1989[b]	Impoundment
Aylesford	44°57'N/ 64°40'W	532	12	1975[b]	Impoundment
Little R	44°57'N/ 64°27'W	250	NA[a]	1967	Impoundment
Milo	43°52'N/ 66°07'W	185	10	1947	Impoundment
Salmon R.	44°11'N/ 66°03'W	180	14	1995[b]	Natural
George	44°56'N/ 64°42'W	153	9	1972[b]	Natural
Killam	44°00'N/ 66°05'W	123	8	1981[b]	Natural
Spectacle	44°16'N/ 66°04'W	83	3	1971	Natural

[a] Not available

[b] Exact year of introduction inferred from earliest known catch records.

Table 2. Relative weight (W_r), growth parameters (Brody growth coefficient, K, and L_∞ in mm), maximum observed age (T_{max}), and inferred length at maturity (L_{mat} in mm) for smallmouth bass based on data from Nova Scotia bass tournaments. Values for length at maturity and production-to-biomass ratios derived from life history relationships.

Site	W_r	L_∞	K	T_{max}	L_{mat}	P/B[a]
Grand	82	474	0.184	14	282	0.336
Porters	84	507	0.206	12	310	0.293
Panuke	74	540	0.185	11	331	0.293
Gaspereau	74	531	0.130	14	305	0.378
Black R	74	573	0.126	12	328	0.358
OPP	73	578	0.172	9	362	0.286
Aylesford	77	608	0.123	14	356	0.343
Little R	76	558	0.140	13	328	0.341
Milo	86	425	0.239	10	259	0.323
Salmon R	75	561	0.182	11	346	0.285
George	73	296[b]	0.352[b]	8[b]	245	0.392
Killam	78	489	0.168	11	286	0.345
Spectacle	79	414	0.280	10	257	0.306

[a] Based on Randall and Minns (2000): $P/B=2.64(W_{mat}^{-0.35})$

[b] Two large fish were not included because of lack of fit with von Bertalanffy growth model (see Appendix 1).

Table 3. Survival and mortality parameters for smallmouth bass based on data from Nova Scotia bass tournaments including angler effort and catch rate.

Site	S	Z[a]	F	Exploitation Rate (%)	Angler Effort[b]	Catch Rate[c]
Grand	0.573	0.557	0.167	12.80	9.5	0.25
Porters	0.608	0.498	0.108	8.50	1.0	0.21
Panuke	0.601	0.510	0.120	9.39	2.4	0.20
Gaspereau	0.388	0.946	0.556	58.80	1.9	0.29
Black R	0.484	0.726	0.336	23.88	16.5	0.31
OPP	0.538	0.619	0.229	17.09	10.1	0.22
Aylesford	0.498	0.697	0.307	22.11	10.5	0.18
Little R	0.548	0.601	0.211	15.87	36.6	0.30
Milo	0.389	0.944	0.554	35.86	28.9	0.08
Salmon R	0.450	0.799	0.409	28.15	12.0	0.24
George	0.376	0.978	0.388	24.76	8.6	0.08
Killam	0.509	0.676	0.286	20.77	31.5	0.18
Spectacle	0.538	0.620	0.230	17.14	31.8	0.22

[a] Instantaneous natural mortality was assumed to be equivalent to the median North American value (M=0.39) reported in Beamesderfer and North (1995). For George L we assumed that M was best represented by the 75th percentile of the North American distribution of natural mortality (M=0.59). See methods section.

[b] Angler effort = tournament angler hours per hectare

[c] Catch rate = number of smallmouth bass > 253 mm (TL) caught per tournament angler hour

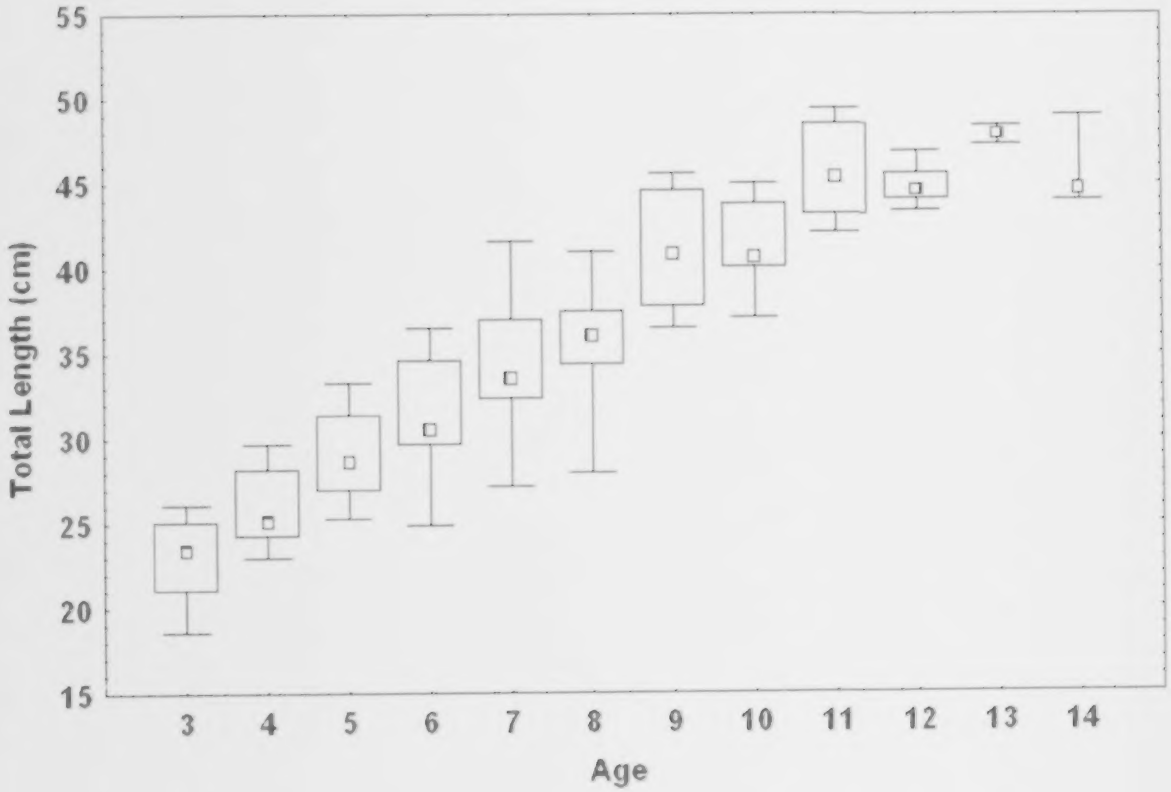
Table 4. Estimates of instantaneous mortality (M_{2*K}) based on the life history invariant of M/K=2. The growth coefficient (K) for each population are listed in Table 3. Instantaneous fishing mortality estimated by $F=Z-M_{2*K}$, assuming M_{2*K} represents natural mortality.

Site	M_{2*K}	F	Exploitation Rate (%)
Grand	0.368	0.189	14.5
Porters	0.412	0.086	6.8
Panuke	0.370	0.140	11.0
Gaspereau	0.260	0.686	44.0
Black R	0.252	0.474	33.7
OPP	0.344	0.275	20.5
Aylesford	0.246	0.451	32.5
Little R	0.280	0.321	24.1
Milo	0.478	0.466	30.2
Salmon R	0.364	0.435	29.9
George	0.704	0.274	17.5
Killam	0.336	0.340	24.7
Spectacle	0.560	0.060	4.5

Figure Captions:

Figure 1. Box plot of size (cm, TL) at age for 13 populations of smallmouth bass in Nova Scotia. The small square in each box is the median value with 25th and 75th quartiles represented by lower and upper boundaries of each box. Maximum and minimum values are represented by the upper and lower bars, respectively.

Figure 2. The negative relationship (r = -0.87; N=13) between the von Bertalanffy growth coefficient (K) and asymptotic size (L_{∞}). The regression describing this relationship: $Log_e L_{\infty} = 2.97 - 0.55(Log_e K)$; intercept se = 0.15 and slope se = 0.08. Following Charnov (1993), geometric mean regression was used to determine the slope, *h* (0.62).


55
50
45
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35
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Total Length (cm)
3
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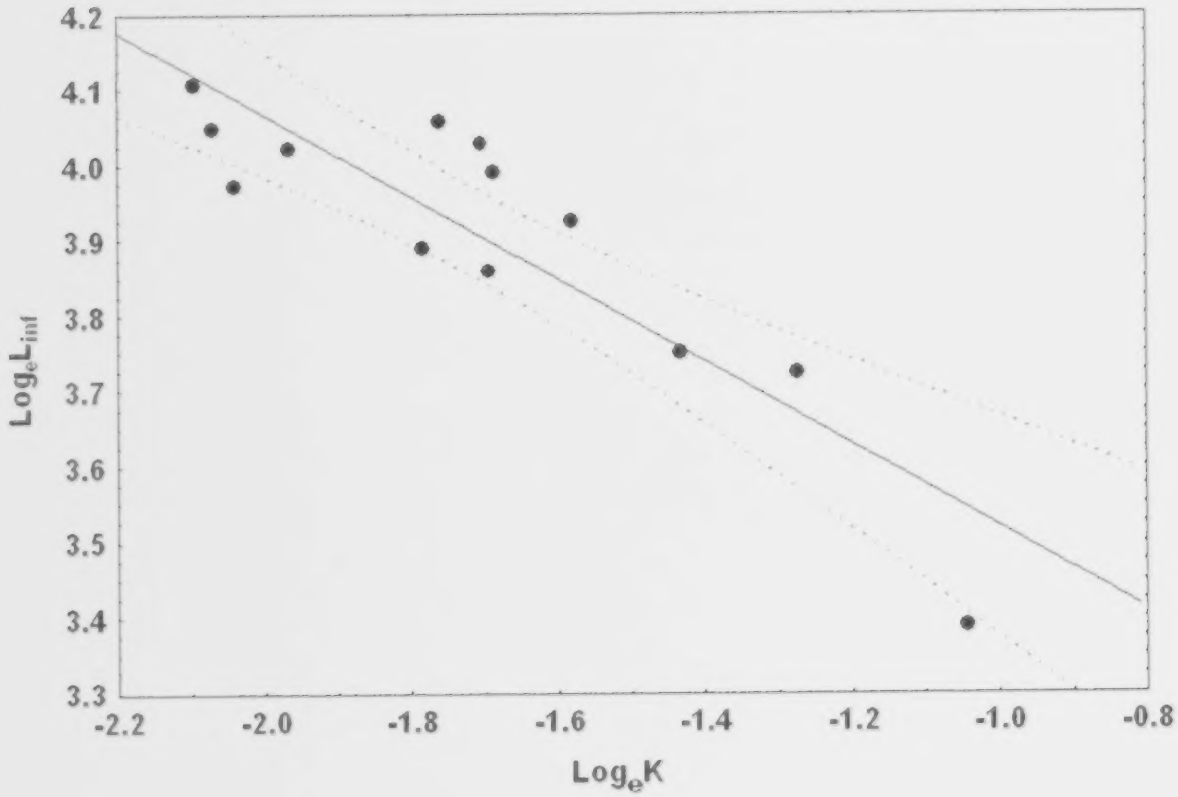
14
Age


4.2
4.1
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3.9
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3.7
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3.5
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Log$_e$L$_{inf}$
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
-0.8
Log$_e$K

Appendix 1. Mean total length of smallmouth bass at different ages based on scale samples.

	Total length at age (mm)											
Site	3	4	5	6	7	8	9	10	11	12	13	14
Grand	225	270	286	296	313	354	379	404	421	454		
440												
Porters	261	286	333	346	370	385	440	450		484		
Panuke	249	297	314	354	374	410	446	445	490			
Gasper.	193	230	257	280	295	336	367	371		443		
446												
Black	189	242	258	299	323	358	408	408	430	448		
OPP	251	282	318	365	416		456					
Aylesf.	217	230	274	302	335	371	437	438	461	469		
490												
Little	210	242	282	305	336	375	401	430	431	456	473	
Milo	243	251	292	316	334	360		400				
Salmon	255	294	327	356	401		450		494			
George	186	232	253	249	272	280			480*	440*		
Killam	234	244	269	296	332	343	365	400	445			
Spectacle	253	279	303	319	354	375	377	400				

* These length data not used in calculating von Bertalanffy parameters